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Scientific Investigations on the Red-Eared Turtle, *Trachemys scripta elegans*

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Scientific Investigations on the Red-Eared Turtle, *Trachemys scripta elegans*

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Preface

These reprints originally appeared in the *Bulletin of the Chicago Herpetological Society, Chelonian Conservation and Biology, Herpetological Review,* and *Journal of Herpetology* and are being provided in this format as a service to Long Term Resource Monitoring Program (LTRMP) partners.

LTRMP interests in the subject matter of these reprints are embodied in the LTRMP Operating Plan[1] in Strategy 2.2.9, *Monitor and Evaluate Wildlife.* These reprints were developed with partial funding provided by the Illinois Natural History Survey, Hatch Act and State of Iowa Funds, and the Upper Mississippi River System Long Term Resource Monitoring Program.

The LTRMP is being implemented by the Environmental Management Technical Center, a U.S. Geological Survey science center, in cooperation with the five Upper Mississippi River System (UMRS) States of Illinois, Iowa, Minnesota, Missouri, and Wisconsin. The U.S. Army Corps of Engineers provides guidance and has overall Program responsibility. The mode of operation and respective roles of the agencies are outlined in a 1988 Memorandum of Agreement.

The UMRS encompasses the commercially navigable reaches of the Upper Mississippi River, as well as the Illinois River and navigable portions of the Kaskaskia, Black, St. Croix, and Minnesota Rivers. Congress has declared the UMRS to be both a nationally significant ecosystem and a nationally significant commercial navigation system. The mission of the LTRMP is to provide decision makers with information for maintaining the UMRS as a sustainable large river ecosystem given its multiple-use character. The long-term goals of the Program are to understand the system, determine resource trends and effects, develop management alternatives, manage information, and develop useful products.

[1]U.S. Fish and Wildlife Service. 1993. Operating Plan for the Upper Mississippi River System Long Term Resource Monitoring Program. Environmental Management Technical Center, Onalaska, Wisconsin, Revised September 1993. EMTC 91-P002R. 179 pp. (NTIS #PB94-160199)

Melanism in the Red-eared Slider (*Trachemys scripta elegans*)

by

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Melanism in the Red-eared Slider (*Trachemys scripta elegans*)

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Melanism in the pond slider, *Trachemys scripta*, has been the subject of several investigations. Carr (1952) described the pattern of changes associated with the phenomenon and reviewed the taxonomic confusion it created among early naturalists. Cagle (1950) described the changes that occur during the transition from the premelanistic state to the fully melanized condition for male red-eared turtles (*T. s. elegans*, hereafter called *elegans*). McCoy (1968) described the development of melanism among *elegans* from Oklahoma and emphasized color changes that occur in the plastrons of both sexes. Lovich et al. (1990) discussed the physiological and morphological correlates that accompany shell coloration changes of male yellow-bellied turtles (*T. s. scripta*, hereafter called *scripta*). They pointed out that previous studies are difficult to compare because of imprecision in the definition of a melanistic male. They also noted that melanism among males is not strictly related to body size but varies among sites from the same region as a function of site-specific growth rates, and that the onset of melanism is related to site-specific female size at maturity. Herein, we compute mathematical models of the relationships first pointed out by Lovich et al. (1990) that predict the mean plastron lengths of melanistic males and the mean ages at which full melanism is attained for *elegans*.

We collected turtles for this study from Airport Lake (sec. 3, T48N, R5E), Brickhouse Slough (sec. 21, T48N, R6E), Ellis Lake (sec. 26, T48N, R7E), Ellis Bay (sec. 26, T48N, R7E), and Maple Slough (sec. 31, T48N, R7E) all of which are backwaters of the Mississippi River in St. Charles County, Missouri. We also collected turtles from Turkey Slough (sec. 32, T48N, R3E, Lincoln County, Missouri) and Piasa Island (sec. 31, T6N, R10W, Madison County, Illinois), both backwaters of the Mississippi River. Additional turtles came from two backwaters of the Illinois River, Stump Lake (sec. 9, T12S, R1W, Jersey County, Illinois) and Swan Lake (sec. 31, T12S, R1W, Calhoun County, Illinois). At six of these locations (Airport Lake, Brickhouse Slough, Piasa Island, Ellis Lake, Stump Lake, and Turkey Slough), we determined mean plastron lengths for melanistic males and for three year old males and females. At the other three locations (Ellis Bay, Swan Lake, and Maple Slough), we also estimated the age of melanistic males.

We collected turtles at Ellis Bay, Ellis Lake, Maple Slough, and Stump Lake with baited hoop traps (Leg-

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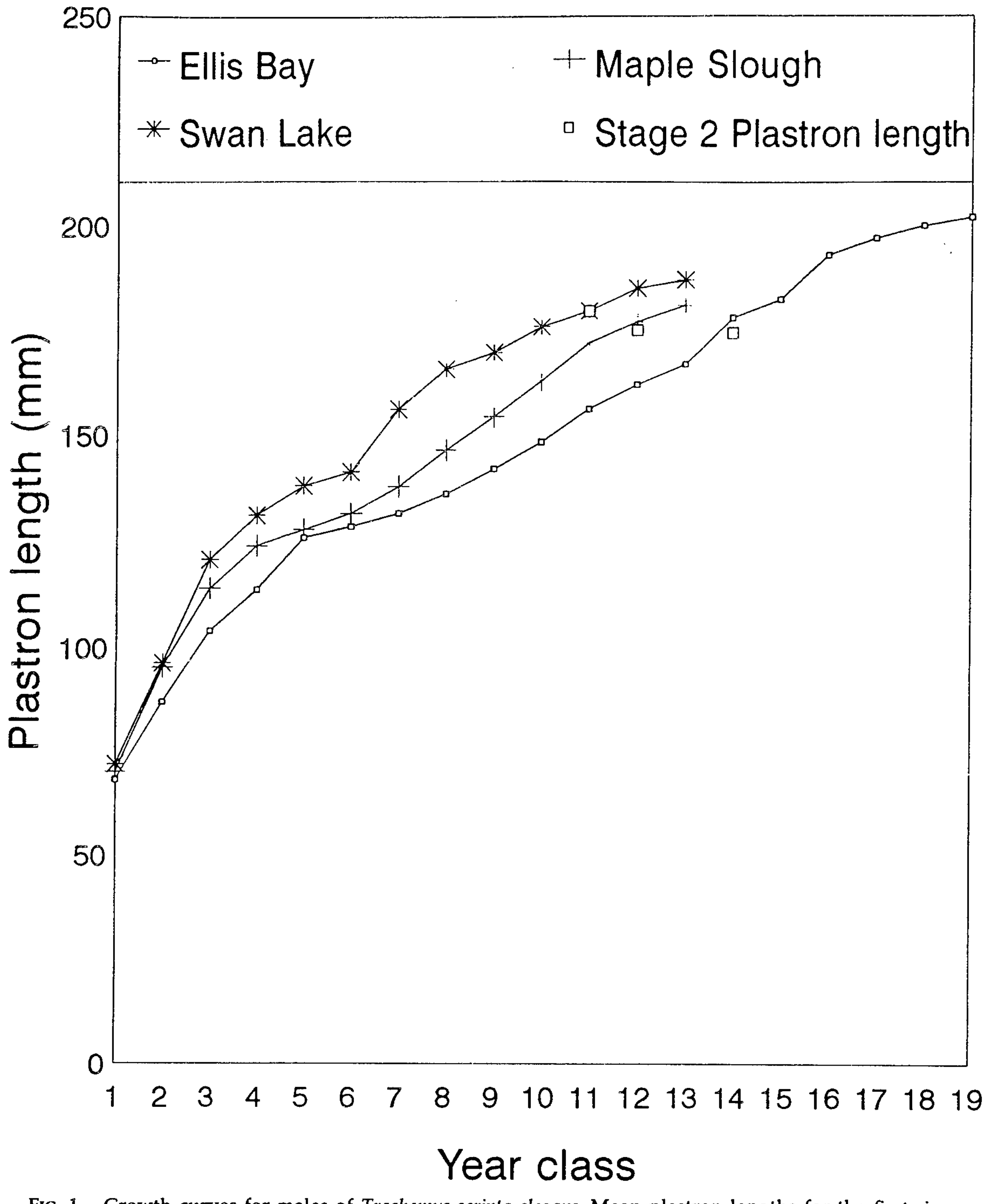

FIG. 1. Growth curves for males of *Trachemys scripta elegans.* Mean plastron lengths for the first six year classes for all three sites are based on plastron lengths determined from counts and measurements of turtles possessing a complete set of annuli. Mean plastron lengths for remaining year classes were estimated using Sexton's method. Mean plastron length of turtles with stage 2 melanism shown for each site (open square).

→

FIG. 2. (a): Regression of estimated age of melanistic males against mean plastron length of third year males based on three locations where age could be estimated. (b): Regression of mean plastron length of melanistic males against mean plastron length of third year females for turtles from all nine locations.

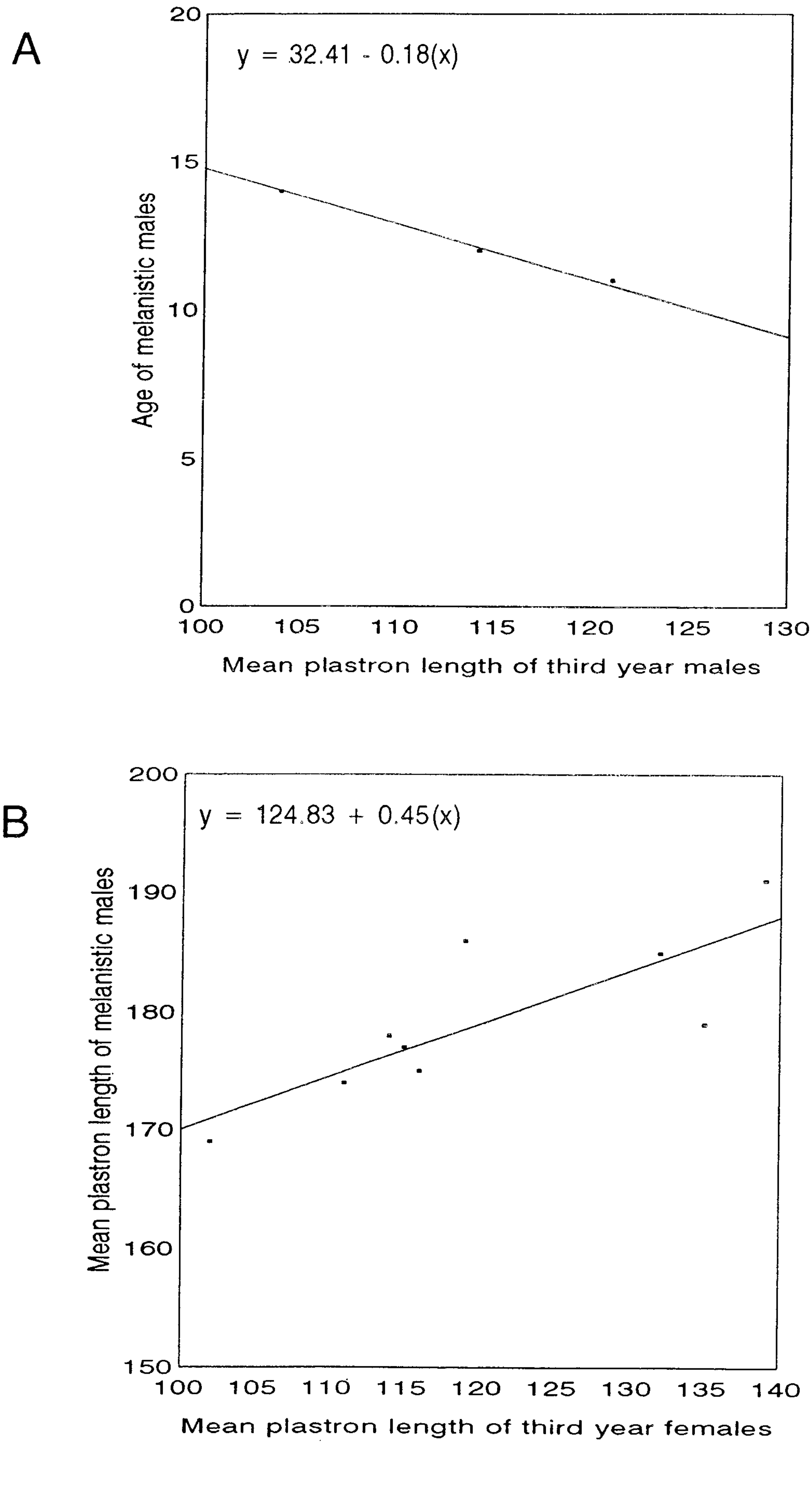
A
y = 32.41 - 0.18(x)
Age of melanistic males
0
5
10
15
20
100
105
110
115
120
125
130
Mean plastron length of third year males
B
y = 124.83 + 0.45(x)
Mean plastron length of melanistic males
150
160
170
180
190
200
100
105
110
115
120
125
130
135
140
Mean plastron length of third year females

TABLE 1. Sample sizes and mean plastron length for third year females, third year males, and melanistic males for nine locations on the lower Illinois River and pool 26 of the Mississippi River.

	Third year females		Third year males		Melanistic males	
Location	(mm)	N	(mm)	N	(mm)	N
Airport Lake	119	5	114	12	186	5
Brickhouse Slough	115	9	109	8	177	5
Piasa Island	102	8	104	6	169	5
Ellis Lake	132	56	103	24	185	6
Stump Lake	139	24	109	11	191	14
Turkey Slough	114	16	103	9	178	6
Ellis Bay	111	62	103	22	174	25
Swan Lake	135	29	121	15	179	70
Maple Slough	116	13	114	7	175	11

ler, 1960). With the exception of Maple Slough and Stump Lake, we also collected specimens with unbaited minnow fyke nets, and unbaited Wisconsin style fyke nets at each location. We used trammel nets that measured 91 m long with outside panels of 36 cm mesh and an inner panel of 8 cm mesh to collect further specimens from Swan Lake. Trap bait consisted of dead fish, primarily gizzard shad (*Dorosoma cepedianum*) or canned sardines (Ernst, 1965).

We divide the developmental pattern (Carr, 1952; Cagle, 1950; McCoy, 1968) of melanism in males into three stages that we define as follows: Stage 0: No melanistic changes present; all costal (C) scutes with well developed yellow bars; carapace greenish colored; head and legs with bright yellow stripes; and a bright red postorbital mark.

Stage 1: At least some melanistic changes have occurred. These may be limited to loss of the yellow bars on right/left C4 or may be advanced to the point that the carapace is colored brown, tan, or yellow-brown, with black borders developed along costal and vertebral margins; head and leg coloration may be unchanged or the yellow stripes on the head may be obscured by brown coloration, postorbital bar brick red to brownish red but still distinct; and front legs retain bright yellow stripes.

Stage 2: Carapace is brown, tan, or yellow brown; black borders developed along costal and vertebral margins; yellow stripes on head and postorbital mark become obscured by brown reticulations; and stripes on the front legs are obscured by brown coloration.

We restrict the definition of the term "melanistic male" to include only stage 2 males. Males in other stages are considered nonmelanistic (stage 0) or premelanistic (stage 1) by us. The fact that previous authors have differed in their use of the term melanistic complicates comparison of our data with previously published measurements of "melanistic" specimens of *elegans* from other areas. None of the females that we observed could be classified as stage 2 because none showed significant pigmentation changes in the head pattern. Except for use of site-specific growth data, we excluded females from our analysis of melanism.

For each turtle, we determined sex (Cagle, 1948, 1950), and straight-line plastron length along the midline of the plastron to the nearest mm with vernier calipers for smaller individuals and with a millimeter rule for larger specimens. The methods used to determine growth follow Tucker (1978) for turtles with a complete set of annuli (ages 1–6 yr) and Sexton (1959) for turtles with incomplete sets of annuli (ages >6 yr).

Because no melanistic male retained a complete set of annuli, we constructed growth curves (Fig. 1) from sets of annuli (years 1–6) and from Sexton estimates (years 7+) to estimate the age of melanistic males for turtles from Ellis Bay, Swan Lake, and Maple Slough. We collected too few older males with incomplete sets of annuli at the other locations to construct such estimates of age of melanistic males. The point where the mean plastron length for stage 2 males intersects the curve (Fig. 1) is an estimate of the age an individual turtle might be expected to be after reaching this plastron length at each site.

Because previous studies have associated attainment of melanism with both male and female growth rates, we chose the mean plastron length following three full seasons of growth as an indicator of site-specific growth rates among males and females. At the sites we studied, growth slows at this age in males with the attainment of sexual maturity (Cagle, 1950). Even though female growth continues at this rate into the fifth year, we used the third year for females as well because of the larger sample sizes and the comparability of the data to those used for the males.

We used the Shapiro-Wilk test (SAS Institute, 1988) to test for normality in the distribution of plastron lengths for three year old males and females and plastron lengths of melanistic males. Because P values ranged from 0.1210 to 0.5333, we used parametric statistics for further analysis.

Correlation analysis was performed on the data matrix containing mean plastron lengths of third-year males and females (Table 1), estimated age of stage 2 males (Fig. 1), and mean plastron length of males at attainment of stage 2 for each sample (Table 1). Because no stage 2 male retained annuli (making it impossible to determine exact age or third-year plastron length), correlation analyses were performed on the means for the pooled sites. Use of means reduces the sample size for each correlation to three for comparisons including age of melanistic males and to nine for those not including age of melanistic males. For correlations that were statistically significant, we computed simple linear regressions for the pooled sites, with the mean third-year plastron length of males as the independent variable.

Trap bias (Ream and Ream, 1966) could be a factor in the results. The relatively large number (N = 70) of stage 2 males caught in Swan Lake as compared to the other sites (N = 5 to 25 per site) may be due to bias towards larger turtles introduced by use of large mesh trammel nets. However, we do not use the relative percentages of particular stage turtles in this study. Instead, we use mean plastron lengths as the basic unit of comparison.

The mean age estimated for stage 2 males was 14 yr for Ellis Bay, 12 yr for Maple Slough, and 11 yr for Swan Lake (Fig. 1). Correlation analysis yielded statistically significant ($P < 0.05$) correlation coefficients

for mean age of stage 2 males with mean plastron lengths of males after three seasons of growth (r = −0.99805) and for mean plastron length of stage 2 males with mean plastron lengths of females after three seasons growth (r = 0.81543).

We derived two models for significant correlations using regression analysis. The first quantifies the correlation between mean age of stage 2 males and the site-specific growth rate for males as indicated by the mean plastron length males reach after three full seasons of growth (Fig. 2a). This model has an F value of 255.15 ($P = 0.0398$) with $R^2 = 0.9961$. The second quantifies the correlation between mean plastron lengths of stage 2 males and the site-specific growth rates of females as indicated by the mean plastron length females reach after three full seasons of growth (Fig. 2b). This model has an F value of 13.89 ($P = 0.0074$) with $R^2 = 0.6649$.

For most turtles, physical milestones such as the attainment of sexual maturity in males and females are related to either size or age (Gibbons et al., 1981). This is not necessarily the case with melanism. Lovich et al. (1990) previously noted this but did not quantify the relationships mathematically. In our preliminary analysis, the correlations we found between site-specific female growth rates and mean plastron lengths of stage 2 males, and between age of stage 2 males and mean plastron lengths of males after three full seasons of growth, concur with those found by Lovich et al. (1990). Furthermore, our conclusion that male *elegans* attain stage 2 between ages 11 to 14 yr, based on age estimates using Sexton's method, is similar to means of 14.8 and 8.8 yr for slow- and fast-growth *scripta* determined by Lovich et al. (1990) from known-age males, even though the latter used a broader definition of melanism. This is important because the models outlined herein are based on means from each site in order to estimate age at stage 2. This effectively reduces the sample size to the number of sites sampled rather than the number of turtles caught. Although the number of sites examined is small, the close agreement between our results and those reported by Lovich et al. (1990) is worthy of note.

The factors that produce the relationships reported by Lovich et al. (1990) for *scripta* and confirmed by us for *elegans* are at present unknown. We speculate that they may be associated with competition among melanistic males for mates because previously published studies suggest that males may interact with each other and females may prefer melanistic males as mates. For instance, Lardie (1983) reported aggressive interactions among free-ranging melanistic male *elegans* in Oklahoma. We also noted a distinct behavioral difference between stage 1 and stage 2 males. The very active stage 2 males made determined attempts to bite when handled, whereas relatively impassive stage 0 and stage 1 males seldom attempted to bite during handling. Cahn (1937), Carr (1952), and Cagle (1950) reported similar observations for *elegans*. However, Cagle (1950) reported that among captive males there was only a "slight tendency toward fighting" (Cagle, 1950, p. 37) even when more than one turtle was competing for a mate. He did report that larger males were more successful and attributed that to their bulk. If encounters between melanistic males lead to aggressive behavior by one or both turtles towards the other, while encounters between melanistic and nonmelanistic males do not, then it may be that males must exceed a certain size in order to be likely to succeed in such encounters. Males smaller than that size are not likely to be successful and becoming melanistic at a smaller size would result in energy being expended to escape larger melanistic males rather than in successful courtship of females.

Cagle (1950) suggested that females preferred melanistic males as mating partners. Lovich et al. (1990) reviewed the possible intersexual and intrasexual significance of melanism in *T. scripta* and suggested that melanism may be an important mode of communication. To the female, it may communicate male mating availability (Lovich et al., 1990) and may facilitate species recognition by both sexes (Moll et al., 1981). Thus the correlation with age at stage 2 with mean male site-specific growth rates would be expected because site-specific growth rates vary, whereas the optimum size to attain stage 2 remains fixed. Consequently, at slow-growth sites (Lovich et al., 1990) males reach optimum size at a greater age than do males from fast-growth sites.

The correlation between female but not male site-specific growth rates and the size attained at stage 2 by males has yet to be explained. It may be related to the fact that some of the males begin to mature after two years (Cagle, 1950). These turtles grow more slowly than turtles whose maturity is delayed into the third or fourth season of growth. Females at a particular site grow at relatively constant rates into their fifth or sixth year, with resulting low variance in measures of growth rates. If this explains our observations and those of Lovich et al. (1990), then larger samples that allow separation of males into cohorts based on the age at which maturity occurs may show that male growth rates are also correlated with size at attainment of stage 2 melanism.

The models when used together will simplify the process of estimating the age of stage 2 males in the study area. In order to estimate the age of melanistic males at a particular site, the mean plastron lengths of both males and females following three full seasons of growth must be known. Model 1 can then be used to estimate the age of stage 2 males. Model 2, which estimates the mean plastron length of stage 2 males, can be used to determine the amount of confidence that can be placed on the estimate of age from model 1. If sufficient stage 2 males are available from the site, then the actual mean plastron length can be determined and compared to the one computed using model 2. If these agree, then greater confidence can be placed on the calculated estimate for the age of stage 2 males.

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Salvage of Eggs from Road-killed Red-eared Sliders, *Trachemys scripta elegans*

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Salvage of Eggs from Road-Killed Red-Eared Sliders, *Trachemys scripta elegans*

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Both aquatic and terrestrial turtles of many species are known to make nesting migrations (see Cagle, 1950 and Gibbons et al., 1990 for *Trachemys scripta*; also Ernst and Barbour, 1989, and Gibbons et al., 1990, for a review). Among the hazards faced during such migrations are encounters with vehicular traffic when females attempt to cross roads (e.g., Iverson, 1977, 1980; Obbard and Brooks, 1980; Diemer, 1986; Galbraith et al., 1989). Frequently such encounters are fatal for the female and her unlaid eggs. Much biological data can be gathered by careful examination of such road-killed turtles. Iverson (1980) noted the value of road-killed tortoises (*Gopherus polyphemus*) for use in studies of reproductive ecology of the species. Galbraith et al. (1989) gathered information on the snapping turtle (*Chelydra serpentina*) from road-killed specimens.

Relatively few studies have reported results from attempts to salvage and incubate eggs from road-killed turtles, but see Lardie (1976) for the painted turtle (*Chrysemys picta*), Iverson (1977, 1980) for the gopher tortoise (*Gopherus polyphemus*) and the box turtle (*Terrapene carolina*), and R.C. Wood (*pers. comm.*) for the diamondback terrapin (*Malaclemys terrapin*). I chose to use the red-eared slider (*Trachemys scripta elegans*) as a model to further investigate the salvage and incubation of eggs from road-killed turtles. This study reports results from 32 such turtles, including hatching success for 67 eggs removed from nine turtles.

Materials and Methods. — The study included 32 turtles found struck by vehicular traffic while trying to cross Illinois Route 100 in Jersey and Madison Counties, Illinois. Thirty-one of these were dead or dying when found. One turtle survived to be released. This individual is included as a road-killed turtle because I judged its injuries extensive enough to have caused its death without human intervention.

I travelled the road at least twice daily during the nesting season. Except for instances actually witnessed, the time interval between discovery and striking was estimated by dividing the time interval between trips by 2 (= estimated death time). Estimated death time varied between 1 and 6 hours. Vehicles also kill females returning from nesting. Therefore, only females with evidence of oviducal eggs such as egg shell fragments or intact eggs are included in the study.

Except for the one injured female that survived in which oviposition was induced with oxytocin (Ewert and Legler, 1978), all other eggs were removed from the turtle's body cavity or road surface at the collection site. After placing the eggs in clean, empty, top-locking plastic bags, they were returned to the laboratory, carefully avoiding unnecessary jarring or overheating of the eggs (Limpus et al., 1979).

Wet mass (to 0.01 g) of eggs was determined with an electronic balance, and length and width (to 1 mm) of eggs were measured using vernier calipers. Each egg was uniquely numbered with carbon ink and partially buried in perlite incubation medium (85 ml deionized water plus 150 g perlite), which had been previously placed in plastic Tucker brand modular storage boxes (32 x 19 x 10 cm). Individual eggs were not in contact, and clutches were incubated separately. To retard moisture loss I placed a layer of aluminum foil under the box lid and determined the weight of the box and contents. Once each week the boxes were opened to inspect the eggs for viability (Ewert, 1985) and were rehydrated by adding water until they regained their original weight. Incubation time was defined as the time to date of pipping (Gutzke et al., 1984). Once the first egg of each clutch pipped, a bottomless waxed paper cup was placed over each egg so that hatchlings could be matched to their eggs (Janzen, 1993). Hatchling wet mass (to 0.01 g) was determined with an electronic balance, and hatchling carapacial length and width (to 1 mm) were measured with vernier calipers. Hatchling measurements were made within 24 hours of hatching. Ambient temperature was not controlled, but did not exceeded 34°C nor fall below 24°C, with an average diurnal variation of 7°C. Statistical analyses were performed using the SAS System computer programs (SAS Institute, 1988).

Results. — Of the 32 turtles (31 road-killed and 1 survivor) with oviducal eggs, 23 contained no unbroken eggs. The remaining nine individuals contained between 2 and 21 unbroken eggs. Two individuals with intact carapaces had a mean of 17.5 unbroken eggs and no broken eggs. The other seven individuals with smashed carapaces contained an average of 4.7 unbroken eggs. The difference in number of unbroken eggs is due in part to broken eggs near many of the turtles. I also observed American crows (*Corvus brachyrhynchos*) and fish crows (*C. ossifragus*) removing eggs from the opened carapaces of some turtles. Previously Shealy (1976, for *C. ossifragus*) and Burger (1977, for *C. brachyrhynchos*) reported crow predation on the eggs of the Alabama map turtle (*Graptemys pulchra*) and *Malaclemys terrapin* respectively.

Eggs from the two relatively intact turtles had higher hatch rates (30 of 35 eggs hatched = 85.7%) than eggs from turtles with opened carapaces (13 of 32 eggs hatched = 40.6%); Fisher's exact test, x^2 = 14.8, $P < 0.0001$. The difference is probably due to the fact that the relatively intact turtles had not yet died. One of these survived and was

released. The other died of head injuries shortly after discovery. All turtles with opened carapaces were clinically dead at discovery as evidenced by a lack of coordinated movements when mechanically stimulated.

Of the seven turtles with open carapaces, two, with estimated death times of at least 3 hours, contained a total of five eggs. Only one of these eggs (20%) hatched; the other four failed to develop. The other five turtles, with estimated death times of less than one hour, contained 27 eggs. Of these, 12 (44.4%) hatched, and the remaining eggs failed to develop. However, hatch rates for the two groups are not statistically different (Fisher's exact test, $x^2 = 1.05$, $P = 0.625$), but the sample is very small.

No quantitative or qualitative differences among eggs ($n = 67$) or hatchlings ($n = 43$) existed. The mean initial egg wet mass (10.11 g, range 8.20–11.69, SD 0.76), mean egg width (22 mm, range 20–24, SD 1.17), mean egg length (35 mm, range 33–38, SD 1.48), mean hatchling wet mass (7.29 g, range 6.34–8.48, SD 0.55), mean carapacial width (29 mm, range 26–31, SD 1.19), and mean carapacial length (30 mm, range 27–33, SD 1.22), along with a mean incubation period of 62.1 days (range 60–68 days, SD 1.43) are well within the range for eggs and hatchlings of the subspecies as previously reported by Cagle (1950).

Discussion. — This study documents that a significant percentage (40.6% in the current study) of oviducal eggs removed from road-killed female turtles may hatch. Even though best results were obtained for turtles that did not have the carapace broken open, some eggs from females that had been dead for as long as three hours hatched.

At certain stages in their development, turtle eggs are susceptible to damage by jarring and rough handling (Limpus et al., 1979, but see Feldman, 1983, and Ewert, 1985, for contrary findings). However, they can be remarkably resilient as well. In one instance, where I witnessed the female being struck, four of ten eggs were ejected and bounced down the pavement for 4 to 6 m. Each of these four eggs remained intact, and one of the four hatched.

While *Trachemys scripta elegans* is not an endangered or threatened species, the methodologies for collecting and incubating the eggs are simple and could be applied in programs where endangered or threatened species are concerned (R.C. Wood, *pers. comm.*). Such hatchlings could contribute significantly to conservation programs for endangered chelonians.

Because deaths due to vehicular accidents can be sufficient to reduce populations of endangered species, such as *Gopherus polyphemus* (reviewed by Diemer, 1986) and *G. agassizii* (reviewed by Ruby et al., 1994), subsequent release of hatchlings from salvaged eggs might help mitigate the negative impact of roadways on endangered species of turtles. However, hatching a few eggs offers only minimal compensation as compared to strategies for keeping the adult females alive in the first place. Strategies such as highway barriers (Ruby et al., 1994), warning signs, or speed-reduction devices may be of equal or greater importance in preserving endangered chelonians.

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Unusual Coloration in a Red-eared Slider, *Trachemys scripta elegans*

by

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Unusual Coloration in a Red-eared Slider, *Trachemys scripta elegans*

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Introduction

During the course of fisheries sampling, two of us (FAC, BJK) collected an unusually colored red-eared slider (*Trachemys scripta elegans*) along with many other specimens of normally colored turtles in an unbaited minnow fyke net, set 22 June 1994 at Airport Lake, St. Charles County, Missouri (NW quarter, sec. 3, T48N, R5E). Airport Lake is a backwater of the Mississippi River and is located at river mile 219. Since such color abnormalities are uncommon, having been reported previously only from commercially raised hatchlings (Cagle, 1947), we describe the specimen herein.

Description

The turtle has the following measurements: carapace length = 128.0 mm, carapace width at the junction of second and third vertebrals = 104.1 mm; maximum carapace width which is near the junction of the third and fourth vertebrals = 107.0 mm; plastron length = 123.1 mm; total wet mass = 402 g. The specimen is morphologically a female, having short foreclaws and short tail base with the anus not extending past the posterior margin of the plastron. Males of equal size have elongated claws and an elongated tail base (Cagle, 1948). The turtle is a three-year-old based on counts of the well preserved annuli on the plastron.

The shell (carapace + plastron + bridge) shows no sign of the green coloration that is characteristic of females of similar size (Smith, 1961). Instead, the carapace is yellowish-tan in color and has black markings (Figure 1A). On the costal scutes, these markings form rounded "V" shapes with the rounded bottom of the V oriented toward the midline of the carapace. Each vertebral scute is marked with a distinct M-shaped black mark that has the top of the M oriented toward the anterior end of the carapace. The marginals, which number 12 per side, are marked with black blotches at their posterior and anterior distal edges. The markings on adjacent marginals are aligned, producing the black blotched appearance. The plastron is yellowish with a single black, solid-colored oval blotch on each scute except for the turtle's left femoral scute which has two such marks (Figure 1B). Such markings are consistent with the developmental pattern found in females reported by McCoy (1968). On each side of the bridge, two black blotches are present and are accompanied by black reticulate markings. The yellowish coloration of the plastron and the underside of each marginal is brighter than the coloration of the carapace.

The soft parts of the turtle (head, neck, limbs, and tail) are normal in color and fit descriptions provided by Cagle (1950), Carr (1952) and Smith (1961). The "ear" is distinct and bright red in color.

Discussion

So far as we can determine, similar coloration has not been previously described from natural populations of the red-eared slider. It most closely approaches the yellow hatchlings reported by Cagle (1947) from individuals gathered for the commercial pet trade in Louisiana. Cagle (1947, p. 1) reported three such turtles from a sample of "more than 30,000 hatchlings." However, the specimen we report has normally colored skin on the body, head and extremities along with some black markings on the carapace and black markings on the scutes of the plastron. The hatchlings reported by Cagle (1947) had no green coloration on the head and no black markings on the carapace or plastron. Apparently, we found yet another genetically or environmentally induced variation not necessarily identical to that reported by Cagle (1947). We speculate that loss or suppression of the ability to produce the green coloration usually present on the carapacial scutes produced the color pattern observed.

In some ways, the turtle's coloration resembles that of melanistic males (Cagle, 1948; Carr, 1952). Conant and Collins's (1991, Plate 7) illustration shows the characteristic horn-colored shell found in melanistic males as well as the black borders on each of the carapacial scutes. However, the

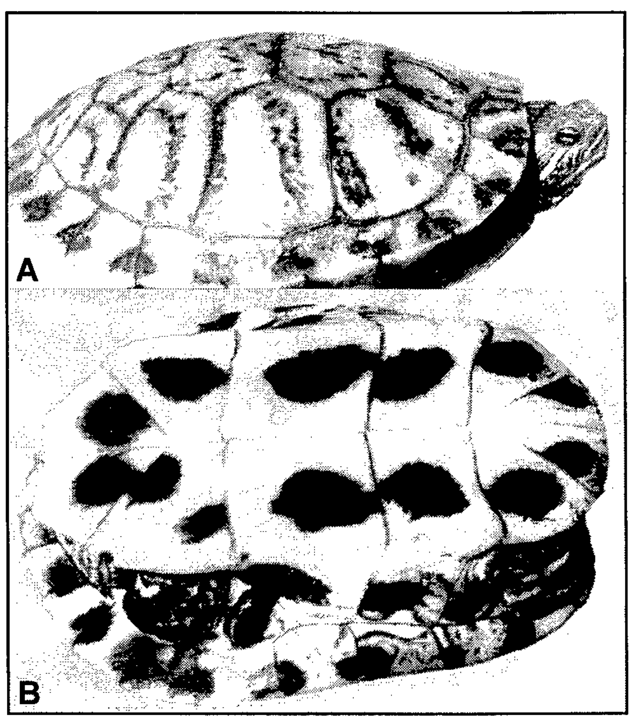

Figure 1. A) View of carapace of a specimen (INHS 11419) of *Trachemys scripta elegans* lacking green color in the shell. B) View of plastron of the same specimen.

turtle that we report is externally a female (Cagle, 1950). Furthermore, her color pattern does not have the pronounced black borders that characterize melanistic males. She also retains the bright yellow and red pattern on the forelimbs and head, which are lost in melanistic males.

The color pattern we report is apparently quite rare in nature. The fisheries program has collected over 1000 *Trachemys scripta* from various areas on the Mississippi River in Pool 26 in the last three years, and all were normally colored. The turtle has been deposited for study in the collections of the Illinois Natural History Survey (INHS 11419).

Acknowledgments

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Fences and Nesting Red-eared Sliders

by

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Fences and Nesting Red-eared Sliders

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Aquatic turtles face many hazards during their nesting excursions. These range from various predators and other natural dangers (reviewed by Ernst et al., 1994) to many hazards associated with human activities (also reviewed by Ernst et al., 1994; Ernst, 1995). Although highway deaths are the most obvious result of these many man-made hazards, other less obvious hazards await nesting females. We were fortunate enough to be able to document and photograph an encounter between a female red-eared slider turtle (*Trachemys scripta elegans*) and a woven-wire fence.

Materials and Methods

This particular turtle was collected at 1120 hr CDT on 5 June 1996, 0.1 km N of the junction of Illinois Route 100 and the Stump Lake access road in Jersey County, Illinois. The turtle was weighed and measured shortly after collection. We induced oviposition with oxytocin (Ewert and Legler, 1978). Eggs were weighed (to 0.01 g) and measured (to 0.1 mm) shortly after oviposition.

We measured the fence mesh and other features of the site where we found the turtle at the time of collection with a mm rule. The turtle was photographed in situ immediately after discovery without altering the site. This turtle was one of ove[r] 250 females collected from a number of nesting areas spaced along Illinois Route 100 in this area. We collected 28 other females at or very near the site where we found the particular female we report here.

Figure 1. Adult female red-eared slider turtle (*Trachemys scripta elegans*) trapped in a woven wire fence near Stump Lake, Jersey County, Illinois.

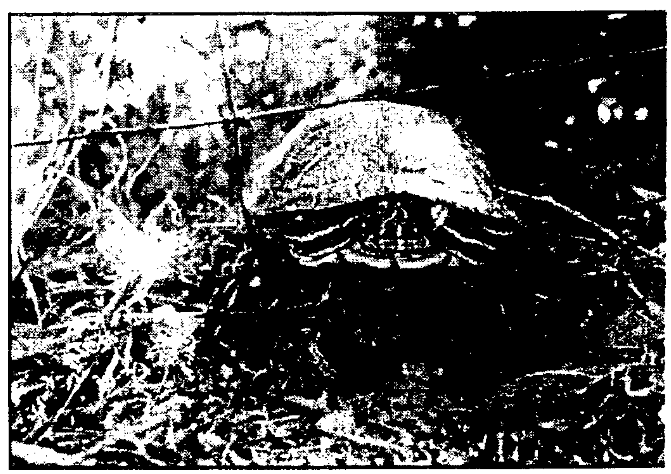

Figure 2. Front view of the same turtle in Figure 1 showing how sh[e] wedged her carapace into the mesh of the fence by angling the shell into the fence. The fence mesh is 171 mm wide and 103 mm high.

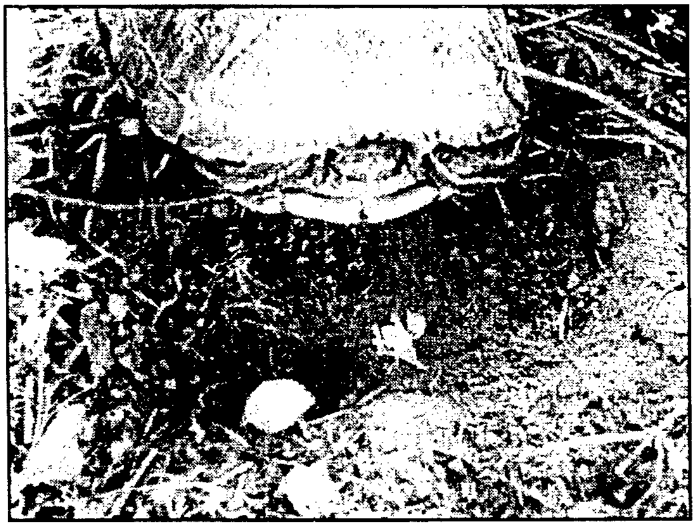

Figure 3. Oblique view of the same turtle in Figure 1 showing the holes dug by the front feet as she tried to pull her carapace through the fence mesh.

Results and Discussion

We found the turtle tightly jammed into the mesh of a woven-wire fence (Figure 1). The fence mesh measured 103 mm high × 171 mm wide. The turtle was a gravid female measuring 231 mm in carapace length, 217 mm in plastron length, 176 mm in maximum carapace width, and 92 mm in maximum carapace height. Her gravid mass was 1.9 kg. She laid 13 apparently normal eggs, which averaged 11.13 g in mass, 35.1 mm in length, and 23.1 mm in width.

The fence in which the turtle became trapped was less than 10 m long and was open at either end. Apparently, the female left Stump Lake, which was flooded at the time, and crossed Illinois Route 100 onto a mowed lawn to nest as do other turtles at this site. She apparently entered a small wood-lot adjacent to the usual nesting site for turtles that cross the road at this location. Upon leaving the wood-lot, she became trapped in the fence before she found a suitable place to lay he eggs. Although the mesh of the fence was high enough to allow her carapace to pass through, the width of the mesh was not (i.e., 171 mm wide mesh vs. a carapace width of 176 mm) When she slightly angled her carapace to complete passage through the fence, she became firmly wedged into the mesh o the fence (Figure 2).

Apparently, the turtle was trapped for some time because she had dug two holes under her front feet as she tried to pull herself through the fence (Figure 3). These holes measured 7 mm deep under the left front foot and 60 mm deep under the right front foot. We believe that this turtle would not have been able to escape the fence had we not happened along.

Clearly, woven wire fences can be hazardous for nesting female turtles when the mesh is large enough for the turtle to enter but too small for her to get through once she has started into the mesh. Although we found only this single instance, such accidents may be more frequent than is currently realize Protective fences (e.g., Brooks, 1995) in management and conservation areas where nesting female turtles may be prese should either have a mesh size large enough to allow passage large adult turtles or narrow enough to discourage the attempt

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Trachemys scripta elegans (Red-eared Slider) Reproduction

by

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TESTUDINES

TRACHEMYS SCRIPTA ELEGANS (Red-eared Slider) **REPRODUCTION.** I report the largest known clutch for *Trachemys scripta elegans* and one of the largest known for the Emydinae (*sensu* Ernst and Barbour 1984. Turtles of the World. Smithsonian Inst. Press, Washington, D.C., 313 pp.). The female (250 mm plastral length, 3125 g gravid body mass) was collected crossing the Illinois River Road, near Pohlman Slough in Calhoun Co., Illinois, USA (NE1/4 Sec. 15, T13S, RlW) on 16 June 1995. The largest clutch reported range-wide for this species (excluding tropical races) is 25 eggs (Ernst et al. 1994. Turtles of the United States and Canada. Smithsonian Inst. Press, Washington, D.C., 578 pp.). The clutch reported herein is equivalent to the largest clutch reported for tropical races (Moll and Moll 1990. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 152–161. Smithsonian Inst. Press, Washington, D.C.). Among other Emydinae, only *Pseudemys nelsoni* (31 eggs/clutch) and *P. rubriventris* (35 eggs/clutch) have been reported to lay larger clutches. Clearly, this is an exceptionally large clutch for *T. s. elegans* which has been reported to lay between 2 and 23 eggs per clutch (Ernst et al. 1994, *op. cit.*)

The 30 eggs averaged 12.09 g mass (range = 8.71–13.51 g, SD = 1.04 g), 35.9 mm long (range = 35.0–40.1 mm, SD = 1.12 mm), and 23.9 mm wide (range = 21.2–25.0 mm, SD = 1.14 mm) shortly after induced oviposition (Ewert and Legler 1978. Herpetologica 34:314–318). After 70 days of incubation at ambient temperatures ranging between 22.1 and 34.6°C, 29 of the eggs hatched. Hatchlings averaged 9.30 g mass (range = 7.92–10.26 g, SD = 0.53 g), 32.4 mm carapacial length (range = 30.9–34.2 mm, SD = 0.78 mm), 31.3 carapacial width (range = 29.0–33.1 mm, SD = 1. 11 mm), and 31.1 mm plastral length (range = 29. 6–32. 6 mm, SD = 0.87 mm) .

Submitted by **JOHN K. TUCKER**, Illinois Natural History Survey, Long Term Resource Monitoring Program Pool 26, 4134 Alby Street, Alton, Illinois 62002, USA.

Two Examples of Twinning in the Red-eared Slider (*Trachemys scripta elegans*)

by

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Two Examples of Twinning in the Red-eared Slider (*Trachemys scripta elegans*)

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Introduction

Twinning in turtles is not a common phenomenon. Consequently, turtle twins tend to be reported in the literature (see Hildebrand, 1938; Tucker and Funk, 1976; Plymale et al., 1980; and Eckert, 1990, for reviews). A number of cases have been reported for *Trachemys scripta*, including examples of conjoined twins (Plymale et al., 1980; Padgett, 1987) and double-yolked eggs (Tucker, 1995).

During the course of a study of reproduction and twinning in *T. s. elegans*, living examples of a conjoined set of twins and a set of subequal sized twins hatched. Because such twins are uncommon, I report on them herein. They were among several sets of twins observed.

Materials and Methods

Both females that produced the eggs containing twins were collected at Swan Lake, a contiguous backwater of the Illinois River, in Calhoun County, Illinois. The female that produced the conjoined twins was collected on 1 June 1995. She had a plastral length of 202 mm and weighed 1.525 kg. The female that produced the other set of twins was collected 3 June 1995. She had a plastral length of 227 mm and weighed 2.025 kg. Both females were marked and released after oviposition was induced with oxytocin (Ewert and Legler, 1978). All eggs in the two clutches were weighed on a Sartorius electronic balance to 0.01 g.

Figure 2. Anterior view of the conjoined twins shown in Figure 1.

Figure 1. Dorsal view of conjoined *Trachemys scripta elegans* twins. Carapace length is 25.7 mm.

Eggs were incubated on vermiculite (300 g vermiculite : 350 ml water) at ambient temperatures that ranged from 16 to 36°C with a daily average of 24°C. In both cases, hatchlings pipped the eggs and left the egg shells unaided. Once hatched all turtles including the twins were weighed to 0.01 g and the carapace lengths measured to 0.1 mm.

Results and Discussion

The data gathered for the twins and their siblings are summarized in Table 1. These data and data on other sets of twins will be presented in greater detail in a forthcoming paper on twinning in turtles by the author and Dr. Fredric J. Janzen.

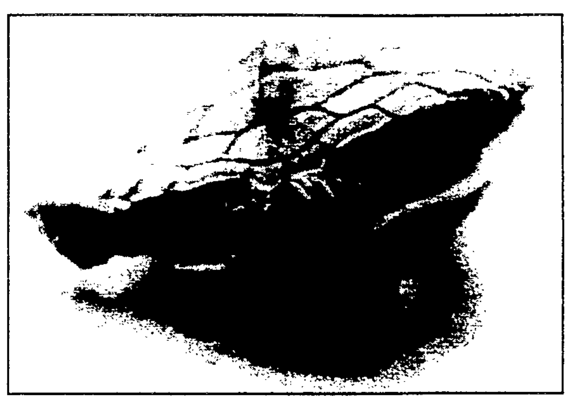

Figure 3. Posterior view of the conjoined twins shown in Figure 1.

Table 1. Morphometric details on two unusual sets of twins and their siblings of the red-eared slider, *Trachemys scripta elegans*, from Illinois. All masses in grams and all lengths in millimeters. CL = carapace length; SD = standard deviation.

	Twins			Other eggs/hatchlings from the clutches containing the twins						
	Eggs	Hatchlings			Eggs		Hatchlings			
	Mass	Mass	CL		Mass		Mass		CL	
				N	mean ± SD	range	mean ± SD	range	mean ± SD	range
Set 1	11.67	8.27	25.7	13	11.10 ± 0.39	10.23–11.62	8.70 ± 0.28	8.21–9.14	31.2 ± 0.70	30.1–32.3
Set 2	12.92	4.59 4.62	25.7 26.6	4	12.93 ± 0.33	12.51–13.24	9.05 ± 0.33	8.60–9.40	32.6 ± 0.71	32.0–33.6

Set 1 = conjoined twins; Set 2 = two individual living twins.

The conjoined set of twins is clearly morphologically abnormal (Figures 1-3). This creature has six legs, two heads, two tails, one shell, and one plastron. It is quite active and remains alive at this juncture. The heads behave independently. It appears from a cursory examination that the left head runs the left legs, whereas the right head runs the right legs. Like many politicians, it tends to be on both sides of an issue simultaneously, and thus makes little progress. I found it remarkable that it was able to pip and escape from the egg unaided (but see Padgett, 1987, for an account of a set of conjoined twins that apparently was able to emerge from a natural nest).

The other twins are morphologically normal but only about half the size of their siblings (Figures 4-5, Table 1). Interestingly, the plastral patterns (Figure 5) of these two turtles differ suggesting that they are dizygotic (i.e., fraternal) rather than monozygotic (i.e., identical). These two turtles were interconnected and apparently shared a single yolk sac (Figure 5).

Acknowledgements

I thank Moynell M. Tucker for assistance in collecting females and eggs. This research was partially supported by the Illinois Natural History Survey and the Upper Mississippi River System Long Term Resource Monitoring Program.

Figure 4. Dorsal view of symmetrical twins of *Trachemys scripta elegans* (small turtles) with a sibling shown for comparison. Carapace of twin on the left is 26.6 mm long.

Figure 5. Ventral view of twins and sibling shown in Figure 4.

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Growth, Reproduction, and Survivorship in the Red-eared Turtle, *Trachemys scripta elegans*, in Illinois, with Conservation Implications

by

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Growth, Reproduction, and Survivorship in the Red-Eared Turtle, *Trachemys scripta elegans*, in Illinois, with Conservation Implications

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ABSTRACT. – **Recaptures of nesting female turtles, *Trachemys scripta elegans*, in Illinois marked more than 20 years ago demonstrate a minimum adult survivorship of 85.2% per year. Age estimates based on plastron length were not reliable. Slow growth of some individuals of known age resulted in 50% underestimates of age. Mean clutch size was identical in known-age turtles and females of unknown age. Recaptured known-age turtles and larger newly marked turtles produced both more and larger eggs than did smaller newly marked turtles. Increased adult mortality of larger turtles whose reproductive output is positively correlated with female size may lead to reduction in number, size, and survivability of hatchlings per female produced in the population because the remaining females are smaller. Programs to compensate for adult losses by head starting hatchlings or otherwise artificially decreasing hatchling mortality may not be as effective in mitigating population decline as programs to prevent adult losses.**

KEY WORDS. – **Reptilia; Testudines; Emydidae; *Trachemys scripta*; turtle; ecology; long-lived vertebrates; survivorship; egg size; hatchling size; reproduction; growth; conservation; Illinois; USA**

Turtles are among the longest lived vertebrates (Gibbons, 1987). However, since few long-term mark and recapture studies have been conducted on chelonians, demographic patterns are known in detail for only six species: *Kinosternon subrubrum*, *Trachemys scripta scripta*, and *Deirochelys reticularia* (Gibbons, 1987; Frazer et al., 1991a); *Chrysemys picta* (Frazer et al., 1991b); *Emydoidea blandingii* (Congdon et al., 1993; Herman et al., 1994); and *Chelydra serpentina* (Galbraith and Brooks, 1987; Congdon et al., 1994). Congdon et al. (1993, 1994) pointed out some of the implications such studies have for the conservation biology of chelonian species. Because increased loss of reproducing adults can only be compensated for by an increase in the relatively high juvenile survival rate in aquatic habitats (e.g., Frazer et al., 1990; Congdon et al., 1993), increases in chronic or acute adult mortality can cause populations to become unstable (Congdon et al., 1993, 1994; Herman et al., 1994).

Because so few long-term studies of survivorship have been published, we report on survivorship, reproduction, and long-term growth of females of the red-eared turtle (*Trachemys scripta elegans*) from west-central Illinois originally marked in the 1970s and recaptured some 20 years later. We suggest that differential loss of larger or older adult females could lead to lowered survivorship of hatchlings produced by the remaining smaller or younger turtles.

MATERIALS AND METHODS

Turtles were collected in or near Stump Lake, a backwater of the Illinois River (Jersey County, Illinois, 39°18'04"N, 90°29'42"W). Turtles were originally collected by D. Moll in the 1970s with baited hoop traps (Legler, 1960) and marked by marginal notching (Cagle, 1939). Plastron length (PL, to 1 mm) was measured, the sex was recorded if possible, and maturity (i.e., adult or subadult) estimated. Turtles were recaptured by J.K. Tucker in 1994 and 1995 at a nesting area near Stump Lake. Because all recaptures were of turtles judged to be adult or subadult females in the 1970s, we did not include the number of juveniles nor the number of males in the total number of turtles available to be recaptured in the 1994–95 collections.

Juvenile and female turtles were also collected in 1994 by J.K. Tucker to determine growth pattern. These turtles were collected in Stump Lake with baited hoop traps, unbaited minnow fyke nets, and unbaited Wisconsin-style fyke nets. Trap bait consisted of dead fish, primarily gizzard shad (*Dorosoma cepedianum*) or canned sardines (Ernst, 1965). We determined age for turtles trapped in 1994 using counts of plastron annuli on the right abdominal scute (Tucker et al., 1995a). Measurements (to 0.1 mm) were limited to annuli that represented a full season's growth (i.e., partial growth in the 1994 season itself was not recorded). No evidence of year-to-year variation in growth was found among females in age classes 3–6 where sufficient turtles were available to test for such variation (Tucker et al., 1995b). Because most males at the study area matured in their third or fourth full season of growth (Tucker et al., 1995a), age classes 1–3 contained all juveniles not identifiable as males based on secondary sexual characteristics.

Original ages at initial capture of 1970s females were estimated by assigning each turtle to the currently determined age class (Table 1) whose mean PL most closely approached the PL at initial capture of that turtle, an adaptation of Sexton's (1959) method. The estimated present age of each turtle then equalled the assigned age class plus the number of years between initial and recent recapture. This method is conservative because it tends to underestimate the age of a particular female (Frazer et al., 1990), in that age is

not necessarily directly size-related and larger turtles may be younger than smaller ones.

To investigate the effect of size and possibly age on reproduction, we divided the sample of newly captured turtles into those with PL less than 211 mm (the approximate asymptote of plastral growth) and those greater than 211 mm. We presumed that small newly captured turtles would include most of the younger turtles, whereas large newly captured turtles would include mostly older turtles more comparable to the recaptured turtles. However, some error is certain as 3 of 9 recaptured turtles known to be at least 20 yrs old were less than 211 mm in PL. We compared reproductive output of the resulting three classes of turtles overall: small newly captured turtles ($n = 68$), large newly captured turtles ($n = 94$), and small and large recaptured turtles ($n = 9$).

We determined egg and hatchling mass (to 0.01 g) with a Sartorius electronic balance. Egg length and width and hatchling carapace length (CL) and width were measured with vernier calipers (to 0.1 mm). Eggs were incubated in various sized plastic boxes. We did not control incubation temperature but recorded it daily with minimum–maximum thermometers placed next to the boxes. Estimated mean incubation temperature ranged from 26.2 to 29.9°C using the method of Godfrey and Mrosovsky (1994).

In 1994 eggs were incubated on moist perlite ranging in water potential from –60 to –189 kPa, with most at –92 kPa as determined by psychrometry. In 1995 eggs were incubated on moist vermiculite of either –150 or –950 kPa, with most on the wettest substrate. Because some of these eggs were used in experiments that caused mortality we did not compare hatching rates. In both years eggs were obtained by inducing oviposition with oxytocin (Ewert and Legler, 1978).

Because two turtles were recaptured nesting in successive years, sample size is 11 for clutch, egg, and hatchling parameters, whereas it is 9 for female parameters based on the most recent recapture. We combined data from 1994 and 1995 recaptures for comparison to combined data for 175 clutches from 162 newly captured female turtles caught nesting at the same site in 1994 ($n = 48$) and 1995 ($n = 127$, including 13 recaptured from 1994).

We used SAS (SAS Institute, 1988) to analyze our data. Statistical analysis for hatchling and egg parameters were of

Table 1. Plastron length by age class determined by annuli counts from juvenile and female *Trachemys scripta elegans* trapped in Stump Lake, Illinois, in 1994.

Year Class	Mean Plastron Length	Range	*n*
1	49.1	42-55	12
2	70.4	60-89	16
3	103.4	88-118	24
4	130.2	106-151	24
5	152.1	130-181	16
6	167.8	151-186	9
7	186.4	173-205	7
8	199.5	180-212	4
9	206.3	198-214	3
10	215.0	208-222	2
11	218.6	218.6	1
12	225.6	225.6	1

the means for clutches from individual turtles. Because some data classes were not normally distributed, we used Spearman's rank correlation and the NPAR1WAY procedure with the Wilcoxon option (SAS Institute, 1988) to perform Kruskal-Wallis tests (= KW with degrees of freedom shown as a subscript) to compare means. In most cases variables were correlated to plastron length of the turtle. However, we did not use analysis of covariance to remove the effect of female body size because our purpose was not to characterize relative reproductive output but to evaluate the actual nature of the eggs and resulting hatchlings produced by the recaptured turtles.

The sequential Bonferroni method was employed to avoid overall type I errors for multiple comparisons (Rice, 1989). In the text means are accompanied by ± one standard deviation followed by the range in parentheses.

RESULTS

Nine of 306 turtles (2.9%) classified as adult or subadult females when initially marked in 1972, 1974, and 1975 were recaptured in 1994 ($n = 5$) and 1995 ($n = 6$) while attempting to nest. We estimated survivorship by back-calculating the survivorship rate required to have 9 turtles remaining from the original cohort of 306 turtles marked in the 1970s. Because we were not able to separate mortality from emigration and because the interval from initial capture to recapture was long, the resulting 85.2% per year survivorship represented an estimate of mimimum adult survivorship.

We estimated long-term growth rates for the 9 recaptured turtles. When initially marked in the 1970s, the 9 recaptured turtles had a mean PL of 181.6 ± 22.6 mm (150–205 mm). When recaptured, they had increased in PL by a mean of 34 ± 18.7 mm (7–68 mm) to a mean PL of 215.5 ± 8.8 mm (204–229 mm) (Table 2). The mean estimated age for the 9 recaptured turtles was 29.1 ± 1.7 yrs (26–32 yrs), whereas the mean interval between initial capture and most recent recapture was 21.7 ± 1.4 yrs (20–23 yrs). During these 21.7 yrs, the PL of the 9 turtles increased at an estimated rate of 1.6 ± 0.8 mm/yr (0.3–3.0 mm/yr).

Recaptured turtles did not differ from newly captured turtles (Table 2) in PL ($KW_1 = 0.59$, p = 0.4441) or body mass ($KW_1 = 0.76$, p = 0.3846). Clutch size ($KW_1 = 0.59$, $p = 0.4419$) and egg size (mass, $KW_1 = 2.29$, $p = 0.1303$; length, $KW_1 = 0.51$, $p = 0.4739$; width, $KW_1 = 3.51$, $p = 0.0609$) of recaptured and newly captured turtles also did not differ nor did hatchling size (mass, $KW_1 = 0.32$, $p = 0.5726$; CL, $KW_1 = 0.64$, $p = 0.4238$, carapace width, $KW_1 = 0.45$, $p = 0.5017$). The recaptured turtles were representative of the population as a whole in both size and reproductive characteristics.

However, female PL was correlated with clutch size ($r = 0.31$, $p < 0.0001$), mean egg mass ($r = 0.51$, $p < 0.0001$), mean egg length ($r = 0.38$, $p < 0.0001$), mean egg width ($r = 0.48$, $p < 0.0001$), mean hatchling mass ($r = 0.43$, $p < 0.0001$), mean hatchling CL ($r = 0.44$, $p < 0.0001$), and mean hatchling carapace width ($r = 0.39$, $p < 0.0001$). Conse-

Table 2. Reproductive parameters of *Trachemys scripta elegans* in Illinois in 1994–95 for 11 clutches from 9 recaptured females compared to 175 clutches from 162 newly captured females with larger and smaller turtle cohorts from the newly captured turtles. Sample sizes for eggs and hatchlings are numbers of clutches produced and hatched, respectively. PL = plastron length, CL = carapace length, CW = carapace width.

Capture Status		Females PL (mm)	Clutch Size (eggs)	Eggs Mass (g)	Eggs Length (mm)	Eggs Width (mm)	Hatchlings Mass (g)	Hatchlings CL (mm)	Hatchlings CW (mm)
Recaptures	mean	215.5	15.1	11.39	36.0	23.0	7.92	30.6	28.8
	SD	8.8	2.5	1.42	2.3	0.7	1.13	1.3	1.5
	range	204-229	12-20	9.52-13.55	32.2-39.6	22.1-24.2	5.96-9.92	28.3-33.1	26.6-31.9
	n	9	11	11	11	11	11	11	11
All New	mean	213.5	14.5	10.55	35.4	22.3	7.63	30.0	28.4
	SD	14.0	3.9	1.60	2.0	1.4	1.17	1.7	1.6
	range	167-240	6-27	6.04-13.45	28.4-39.8	18.0-25.4	3.37-10.02	22.5-33.8	21.8-31.5
	n	162	175	175	175	175	145	145	145
Small New	mean	199.7	12.9	9.61	34.5	21.5	7.09	29.3	27.7
	SD	9.8	3.2	1.69	2.2	1.9	1.30	1.9	1.7
	range	167-210	6-18	6.04-12.88	28.4-38.7	18.0-25.4	3.37-10.02	22.5-33.8	21.8-31.3
	n	68	68	68	68	68	58	58	58
Large New	mean	222.4	15.6	11.15	36.0	22.8	7.99	30.5	28.8
	SD	7.9	3.9	1.21	1.6	1.0	0.92	1.2	1.2
	range	211-240	7-27	8.04-13.45	32.6-39.8	19.3-25.3	5.87-9.84	27.3-32.6	25.4-31.5
	n	94	107	107	107	107	87	87	87

quently, smaller and possibly younger newly captured turtles may have differed from the recaptured turtles, which were known to be more than 20 yrs old.

In accord with the significant correlations between female size and reproductive output, we found that smaller newly captured turtles produced fewer eggs per clutch ($KW_2 = 18.19$, $p < 0.0001$) than did larger newly captured turtles and the recaptured turtles. Eggs of newly captured small turtles were also smaller (mass, $KW_2 = 36.17$, $p < 0.0001$; length, $KW_2 = 20.69$, $p < 0.0001$; width, $KW_2 = 34.53$, $p < 0.0001$) than those of newly captured larger turtles and recaptured turtles. Moreover, the hatchlings from eggs laid by newly captured smaller turtles were smaller than those of newly captured larger turtles and recaptured turtles (hatchling mass, $KW_2 = 17.73$, $p < 0.0001$; hatchling CL, $KW_2 = 18.87$, $p < 0.0001$; hatchling carapace width, $KW_2 = 16.97$, $p < 0.0002$). Clutches, eggs, and hatchlings of larger newly captured turtles and the recaptured turtles (Table 2) did not differ from each other (all KW_1 with $p > 0.05$).

DISCUSSION

While we cannot compute a life table for the turtles in the study area, the 85.2% per year adult survivorship rate for *Trachemys scripta elegans* from Illinois is similar to the 81.7% per year computed for *T. s. scripta* from South Carolina by Frazer et al. (1990) and 83% per year for *Chrysemys picta* from Michigan by Frazer et al. (1991b), but different from those published for *Emydoidea blandingii* (Congdon et al., 1993; 93.5%) and *Chelydra serpentina* (Galbraith and Brooks, 1987, and Congdon et al., 1994; 97%). This is interesting in that the lentic habitats occupied by *T. s. scripta* in South Carolina and the marsh habitat of Michigan *C. picta* differ considerably from the large river backwater habitat of the Illinois *T. s. elegans*. Of course, ours is a minimum estimate of survivorship because we cannot distinguish between the effects of mortality and emigration. However, this was also largely true for the survivorship determinations made by Frazer et al. (1990).

Our data also have a bearing on studies of growth in this and possibly other turtle species. We found some recaptured turtles with a minimum age of 20 yrs to be as small as 204 mm in PL. However, our growth data (by annuli) suggest that the age of such small turtles could also be on the order of 9 yrs (Table 1). Clearly, growth rates constructed from plastral annuli counts are not reliable tools to estimate the age of turtles once they are more than a few years old (Jones and Hartfield, 1995). Furthermore, the error introduced by use of growth rates can be large and would have exceeded 50% in 3 of 9 turtles we recaptured. We suggest that only long-term mark and recapture studies can be used to accurately establish ages for turtles without clearly defined annuli.

Like other studies of known-age turtles (e.g., Congdon et al., 1993, 1994; Herman et al., 1994), we found no evidence of reproductive senescence among the 9 females from which we examined clutches, contrary to the findings of Cagle (1950). Clutch, egg, and hatchling sizes from recaptured turtles were statistically equivalent to the entire sample of turtles. Moreover, they were higher than those observed for smaller turtles, which is consistent with the underlying size correlations.

Our study suggests that the fallacy of a "sustainable harvest of long-lived organisms," so aptly pointed out by Congdon et al. (1993), may be especially true for species such as *T. scripta* where larger turtles produce not only more eggs but larger ones as well. Removal of larger females can only be compensated for by artificially increasing hatchling

and juvenile survivorship with head-starting or predator removal programs, but such programs may be minimally effective since juvenile survivorship in aquatic habitats is often already high in most species (Congdon et al., 1993, 1994).

Removal of larger (and possibly older) adult females might have additional effects not previously pointed out in other studies. First, the number of hatchlings may be reduced because smaller females lay fewer eggs per clutch. Second, because smaller females also lay smaller eggs, hatchling size may decline. The size of hatchlings may directly affect their survival once they leave the nest and grow (e.g., Miller et al., 1987; Brooks et al., 1991; Janzen, 1993a, 1993b; Miller, 1993). In addition, smaller eggs may be less likely to hatch, particularly when incubation conditions are not optimal (Gutzke and Packard, 1985), further reducing recruitment. Thus, both lower recruitment and reduced survivability of hatchlings may occur as a result of differential mortality on large adults in species whose egg size is related to female size. Artificial efforts to increase the number of hatchlings entering the system may be partially compromised if differential adult mortality leads to a reduction in average female size.

The additional effects that we noted are not necessarily limited to *T. scripta*. Positive correlations between one or more egg parameters and female size have been reported for a number of other species and in other studies of *T. scripta* (e.g., Congdon and Gibbons, 1983; Gibbons and Greene, 1990; Mitchell and Pague, 1990). Other species of turtles for which a correlation between female size and one or more egg size parameters has been reported include *Chrysemys picta* (Tucker et al., 1978; Congdon and Tinkle, 1982; Schwarzkopf and Brooks, 1986; Congdon and Gibbons, 1985, 1987; Mitchell, 1985a; Iverson and Smith, 1993; Rowe, 1994, 1995); *Clemmys guttata* (Ernst, 1970) and *C. insculpta* (Brooks et al., 1992); *Deirochelys reticularia* (Congdon et al., 1983; Congdon and Gibbons, 1987); *Graptemys pseudogeographica* and *G. ouachitensis* (Vogt, 1980); *Malaclemys terrapin* (Montevecchi and Burger, 1975); *Chelydra serpentina* (Yntema, 1970); *Gopherus polyphemus* (Landers et al., 1980); *Mauremys leprosa* (Da Silva, 1995); *Testudo hermanni* (Swingland and Stubbs, 1985; Hailey and Loumbourdis, 1988) and *T. graeca* (Hailey and Loumbourdis, 1988); *Sternotherus odoratus* (Risley, 1933; Tinkle, 1961; Mitchell, 1985b) and *S. minor* (Cox and Marion, 1978); and *Kinosternon sonoriense* (Hulse, 1982), *K. subrubrum* (Congdon and Gibbons, 1985), *K. flavescens* (Long, 1986; Iverson, 1991), and *K. hirtipes* (Iverson et al., 1991; Ernst et al., 1994). Although this relationship is better established in some of these species than in others, it seems particularly common among smaller emydid and kinosternid turtles. Several species in these two families are endangered or threatened in parts or all of their ranges. Reduction of large adult mortality, not improvement of hatchling numbers, may be particularly important in designing conservation programs for such species.

Although *Trachemys scripta* is a widely distributed species in North America (Ernst et al., 1994), our findings bear directly on the possible impact of the international trade in this species. As many as 100,000 adult *T. s. elegans* may be collected annually from the wild for "breeding" operations (these "farms" are not closed-end operations, thus the quotes) that supply hatchlings to the international pet market (Warwick, 1986; Warwick et al., 1990). A further 765,000 adults are taken annually for export for human consumption (Warwick et al., 1990). The turtles most in demand for human exploitation, large adult females, are the ones that most populations can least afford to lose if they are to remain stable.

Removal of adult females by artificial or natural means (e.g., Turner et al., 1984; Peterson, 1994) is the functional equivalent of complete clutch failure for the year that the particular female was removed and in all subsequent years. Clutch failure has been shown to lead to lower heterozygosity, higher inbreeding, and greater degrees of co-ancestry in *Chrysemys picta* (Scribner et al., 1993). Consequently, removal of females may also directly impact the genetic base of the population or species which may further slow recovery if exploitation is reduced or regulated.

We suggest that removal of large breeding females may make it more difficult for a population to recover even when exploitation is regulated. Although growth of subadults and small adults into large turtles might ameliorate this loss, it may still take up to 20 years to replace the larger females which we found produced larger hatchlings. Even when such hatchlings are produced, fewer than 2% may survive to an age of 20 yrs (Frazer et al., 1990). Sufficient information is available on the demographics of long-lived vertebrates and the importance of maintaining population age structure and genetic diversity to justify conserving the life-stage segments critical to their continued existence.

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Response of Embryos of the Red-eared Turtle (*Trachemys scripta elegans*) to Experimental Exposure to Water-saturated Substrates

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Response of Embryos of the Red-Eared Turtle (*Trachemys scripta elegans*) to Experimental Exposure to Water-Saturated Substrates

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ABSTRACT. – We exposed early-stage (19–22 day old) and late-stage (39–42 day old) embryos of the red-eared slider turtle (*Trachemys scripta elegans*) that began incubation on substrates of three different water potentials (dry, intermediate, and wet) to water-saturated substrates for five different exposure intervals (1, 6, 12, 24, and 48 hrs). Exposure of early-stage embryos had no significant effect on survivorship for any exposure interval regardless of initial substrate water potential. Exposure of late-stage embryos caused dramatically reduced survivorship when exposure exceeded 12 hrs. Survivorship of eggs exposed for 24 and 48 hrs regardless of substrate was 0%, whereas it was 100% for all other exposure intervals. Exposure of eggs containing early-stage embryos for periods as short as 1 hr allowed rapid uptake of water by the eggs. Water uptake was most pronounced among eggs incubated on the driest substrate even though a narrow range of relatively wet substrates was used. Eggs containing late-stage embryos exposed for less than 24 hrs also took up water, but these changes in egg mass did not translate into increased hatchling mass. Our results support the hypothesis that nest inundation at later stages of embryogenesis is more detrimental to embryonic survival than nest inundation at earlier stages. The nesting season for turtles in the study area coincides with the end of the spring flood pulse as it existed historically prior to modifications of the hydrologic regime by dams. When coupled with unpredictable natural events such as the 1993 flood, altered hydrologic regimes are detrimental to turtles that may time nesting to coincide with decreasing water levels.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Trachemys scripta*; turtle; reproduction; incubation; eggs; embryos; embryonic survival; hydrologic regimes; flooding; Illinois; USA

Although predation is the most commonly noted source of egg mortality among turtles and other reptiles, flooding may also be a significant contributing factor to nest failure. Nest flooding may result from a number of factors. Plummer (1976) noted greater mortality among smooth softshell turtles (*Apalone mutica*) associated with artificially high water levels in the Kansas River. Excessive rainfall has also been associated with nest failures in sea turtles (Hendrickson, 1958; Ragotzkie, 1959; Caldwell et al., 1959; Kraemer and Bell, 1980). Nest flooding due to a hurricane caused 100% mortality among sea turtle nests on beaches closest to the eye of the storm (Milton et al., 1994). Others have reported nest failures in sea turtles due to high tides (Bustard and Greenham, 1968), due to varying lake water levels for a freshwater turtle, *Trionyx sinensis* (Cherepanov, 1990), and due to sudden changes in river levels for another freshwater turtle, *Podocnemis expansa* (Alho and Pádua, 1982). Nest failure due to flooding has been reported for a diversity of other turtle species such as tropical sliders (*Trachemys scripta*, Moll and Legler, 1971), painted turtles (*Chrysemys picta*, Christens and Bider, 1987; Janzen, 1994), ornate box turtles (*Terrapene ornata*, Legler, 1960), and musk turtles (*Sternotherus minor*, Cox and Marion, 1978).

Even though nest flooding may be an important source of hatching failure, relatively few experimental studies adequately explore the variables associated with nest flooding. Some experiments, such as those by Legler (1960) for *Terrapene ornata* and Moll and Legler (1971) for *Trachemys scripta*, used small sample sizes and embryos of varying age, making their results difficult to interpret. In an early experiment using large sample sizes, Plummer (1976) found an incremental increase in mortality associated with increasing immersion intervals for 1- to 12-day-old embryos of *Apalone mutica*, with no survivors after 15 days of immersion.

More recently McGehee (1990) found that hatching success of embryos of *Caretta caretta* was lowest for eggs incubated in sand with 75 and 100% moisture saturation. Kam (1994) exposed 19-day-old embryos of *Pseudemys nelsoni* to immersion for varying periods and found mortality increased with increasing immersion interval.

Although immersion in water has been shown to reduce survivorship in both experimental and empirical studies, it is largely unknown whether embryonic age influences the response of turtle embryos to flooding. Consequently, we exposed early- and late-stage embryos of *Trachemys scripta elegans* to water-saturated substrates for five different exposure intervals, ranging from 1 to 48 hrs. Because hydric environment varies within the same nest and among different nests, we repeated the experiment three times using different substrate water potentials similar to those found in

natural nests in clay soils (Ratterman and Ackerman, 1989). The purpose of the present paper is to report the results of these experiments and to consider the implications that they might have on the ecology, life history, and conservation biology of this and other turtle species.

MATERIALS AND METHODS

We used eggs from 26 clutches, induced by injection of oxytocin (Ewert and Legler, 1978), from red-eared turtles (*Trachemys scripta elegans*) collected while on their nesting excursions in Jersey County, Illinois. We used 120 eggs from 10 clutches on dry substrate, 120 eggs from 7 clutches on intermediate substrate, and 120 eggs from 9 clutches on wet substrate. We uniquely numbered the eggs with carbon ink and determined egg mass (to 0.01 g) with a Sartorius electronic balance. Because we collected the eggs in two groups, the first group began incubation four days before the second group.

For each experiment 120 eggs were randomly divided among 12 Sterilite brand storage boxes (32.5 x 18.1 x 10.6 cm). Boxes were randomly assigned to various exposure intervals, including a control and five experimental intervals (1, 6, 12, 24, and 48 hrs) to a water-saturated substrate (see below) at two different embryonic stages: early-stage = embryos of 19 or 22 days incubation and late-stage = embryos of 39 or 42 days incubation.

We mixed three different perlite substrates by adding various amounts of water to 150 g perlite to produce wet (170 ml water added; –60 kPa), intermediate (85 ml water added; –92 kPa), or dry (27 ml water added; –189 kPa) substrates. Eggs that began incubation on Julian day 155 were kept on wet, intermediate, or dry substrates until day 159 when they, along with eggs started on day 159, were assigned to different exposure intervals. All experimental boxes had freshly made perlite substrate at the start of the experiment (day 159).

We measured initial egg mass on Julian date 155 or 159. We reweighed all early-stage eggs on days 167, 178, 181, 195, and 207, and all late-stage eggs on days 167, 181, 198, 201, and 207. We measured pre-placement egg mass on day 178 for early-stage embryos and day 198 for late-stage embryos, and then reweighed all eggs 36 hrs after the placement in water-saturated substrates began (i.e., day 181 for early-stage embryos and day 201 for late-stage embryos).

We maintained hydration in each box by first determining mass of the box, eggs, and substrates on day 159. We then added sufficient water at each remeasurement date to bring each box back to the original mass after subtracting water taken up by eggs in the box and any losses to the atmosphere. We rehydrated boxes by adding water onto the substrate as evenly as possible without allowing water to directly contact the eggs. All boxes had an aluminum foil covering between the box and lid to retard moisture loss.

We prepared water-saturated substrates by adding 3.7 liters water to 600 g vermiculite into a Sterilite brand box (40 x 27.5 x 15 cm). We used vermiculite for water-saturated substrates because preliminary trials with non-experimental eggs indicated that eggs floated out of comparable water and perlite mixtures. This mixture of vermiculite and water resulted in liquid water at the surface of the vermiculite but not above it. We prepared this mixture freshly for each exposure time. We then placed all eggs for all five exposure intervals (1, 6, 12, 24, and 48 hrs) into the box simultaneously. We positioned eggs so as to completely cover them with water-saturated substrate and did not allow individual eggs to touch each other. At the end of the exposure interval, we brushed off any adhering vermiculite, patted each egg dry, and returned each to its original box. Handling of turtle eggs may (Limpus et al., 1979) or may not (Marcellini and Davis, 1982; Feldman, 1983) influence survivorship. In order to ensure that we subjected experimental and control eggs to equal handling, we also moved control eggs to boxes containing vermiculite mixed in the same proportions as the perlite in their original boxes and returned them to their original boxes after 48 hrs.

During incubation we kept all boxes at the same height and horizontally rotated them once weekly to reduce the effects of temperature gradients. We did not control temperature but recorded it daily beginning on day 161 with minimum-maximum thermometers placed next to the boxes. Estimated mean incubation temperature was 28.9°C determined using the method of Godfrey and Mrosovsky (1994).

Once the first egg pipped, we placed a bottomless waxed paper cup over each egg (Janzen, 1993). We recorded pip date and defined incubation period as pip date minus initial date (Gutzke et al., 1984). Once a turtle left the eggshell, we considered it a survivor. We recorded hatchling mass (to 0.01 g). We opened all eggs that failed to hatch. We did not detect an embryo in any egg that initially failed to whiten (Ewert, 1985). We defined an embryo as killed if its stage of development was consistent with the embryonic age at or after the exposure interval (Yntema, 1968; Kam, 1994). We considered hatchlings that pipped but then died as killed. We prepared a hydrograph using the methods of Nelson et al. (1994), with the nesting season for turtles collected in 1994 superimposed.

Differential mortality could be due either to exposure to water-saturated substrates (Kam, 1994) or to water potential of the incubation substrates (reviewed by Packard, 1991). We addressed mortality caused by exposure effects by comparing survivorship of the subsample of eggs that whitened in combination with an estimation of the age of embryonic death in relation to age at exposure to water-saturated substrates. We staged dead embryos following Yntema (1968).

Statistical Procedures. — Statistical analysis was performed using SAS (SAS Institute, 1988). We used Fisher's exact test (two-tailed) to evaluate differences between survivorship due to substrate and exposure interval effects. We calculated least significant difference (LSD) for each substrate and embryonic age (Figs. 1A–F), using harmonic means because cell sizes differed among exposure intervals

(Snedecor and Cochran, 1986). We used Type III sum of squares to calculate mean squares for both repeated measures analysis and three-way analyses of covariance (ANCOVA).

For tests of hypotheses for between-subject effects in repeated measures analysis and three-way analyses of covariance, one of the variables (i.e., clutch) was a random effect. Consequently, we used the Satterthwaite approximation of denominator degrees of freedom to calculate the expected mean square and *F*-ratio (SAS Institute, 1988; Janzen et al., 1995).

Exposure interval, embryonic age, and the interaction between them were fixed effects, whereas clutch and the interactions between clutch and the fixed effects were random for both repeated measures analyses and mixed models of covariance. Initial egg mass was the covariate in all cases. In some cases the covariate was not a significant source of variation. However, without analysis of covariance (ANCOVA), clutch effects due to egg size differences among clutches are overestimated. Consequently, the covariate was used in all analyses.

For multiple comparisons involved in repeated measure ANCOVA, three-way ANCOVA, and comparisons of least square means, we used the sequential Bonferroni method (Rice, 1989) to identify apparently significant p values insufficient to exclude type I errors at the 0.05 level. For comparisons of the amount of change in egg mass between pre- and post-exposure weighing, we used the REGWQ procedure in SAS analysis of variance (GLM procedure).

RESULTS

Exposure of early-stage embryos to water-saturated substrates had no significant effect on survivorship at any exposure interval regardless of original substrate water potential (dry substrate: $\chi^2 = 4.10, p = 1.00$, 5 df; intermediate substrate: $\chi^2 = 7.38, p = 0.29$, 5 df; wet substrate: $\chi^2 = 5.11$, $p = 0.48$, 5 df). Survivorship for embryos on dry substrate ranged from 87.5% for eggs exposed to water-saturated substrates for 48 hrs to 100% for all other exposure intervals and the control. Survivorship for embryos on intermediate substrate ranged from 87.5% for eggs exposed for 12 hrs to 100% for control eggs and all other exposure intervals except for eggs exposed for 24 hrs, of which 90% of the eggs hatched. Survivorship for embryos on wet substrates ranged from 80% for eggs exposed to water-

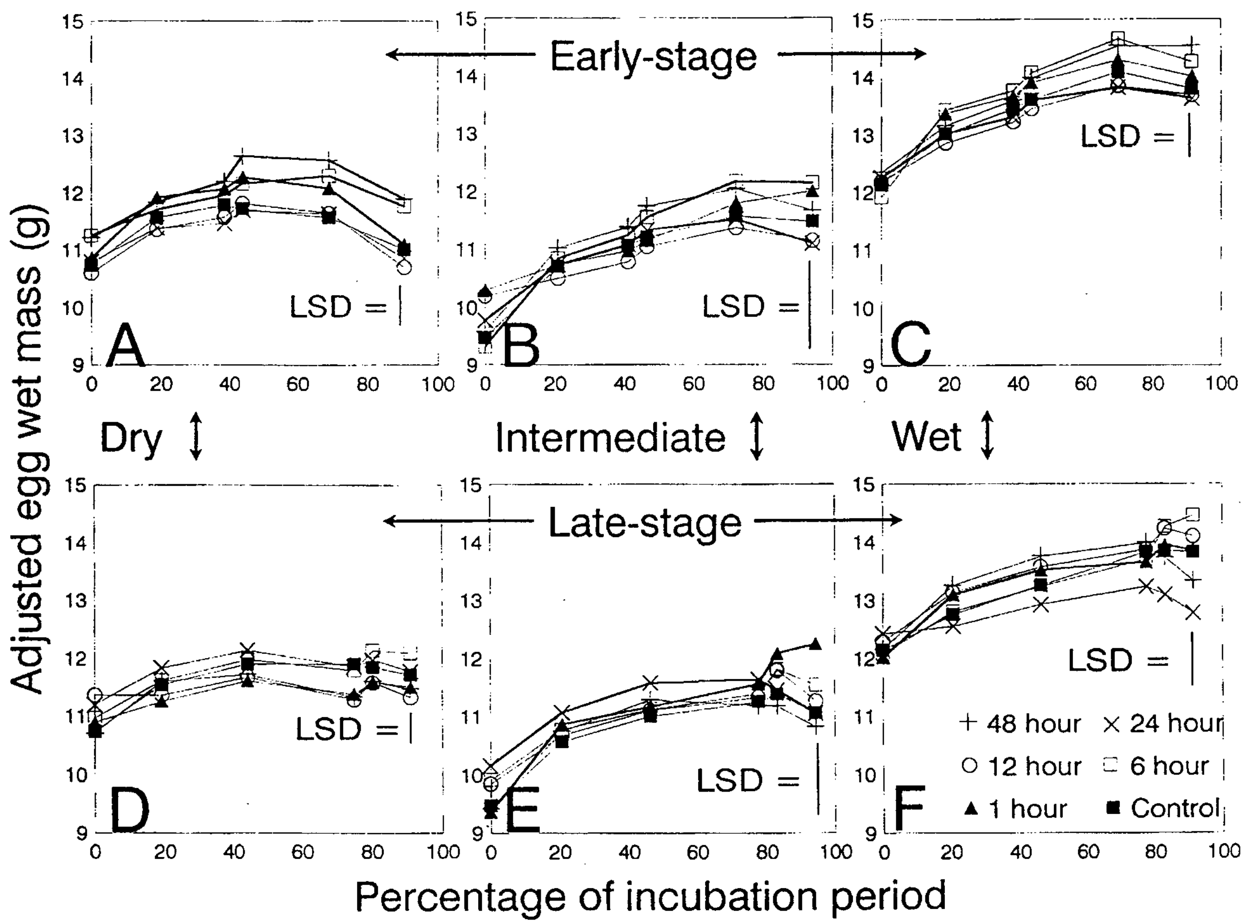

Figure 1. Comparison of changes in egg mass (adjusted wet mass in g) over incubation period (number of days) for exposure intervals to water-saturated substrates at two embryonic ages incubated on three substrates of differing water potentials. **A:** early-stage embryos on dry substrate; **B:** early-stage embryos on intermediate substrate; **C:** early-stage embryos on wet substrate; **D:** late-stage embryos on dry substrate; **E:** late-stage embryos on intermediate substrate; and **F:** late-stage embryos on wet substrate. LSD = least significant difference; except for initial egg mass (at 0% incubation period) all other egg masses are adjusted by initial egg mass.

saturated substrates for 48 and 24 hrs to 100% for all other exposure intervals and the control. Early-stage embryos presumably killed by exposure to water-saturated substrates were all between stages 14 and 15. Exposure of late-stage embryos to water-saturated substrates caused dramatically reduced survivorship when exposure time exceeded 12 hrs. None of the 60 embryos among the 24 and 48 hr exposure intervals survived to emerge from the egg. One individual pipped but died prior to emerging. All other embryos that we identified as killed were between stages 21 and 23. Late-stage embryos were more sensitive to exposure to water-saturated substrates than were early-stage embryos. Survivorship among exposure intervals including the control was different for all three experiments (dry substrate: $\chi^2 = 41.00, p < 0.0001$, 5 df; intermediate substrate: $\chi^2 = 50.00$, $p < 0.0001$, 5 df; wet substrate: $\chi^2 = 51.00, p < 0.0001$, 5 df).

For each exposure interval among early-stage embryos, egg mass immediately after exposure increased, suggesting that exposure to water-saturated substrates for periods as short as 1 hr allowed rapid uptake of water by the eggs (Fig. 1A–C; Table 1). This effect was most pronounced on the dry substrate group where the change in egg mass for all exposure intervals was significantly greater than for the control, and the change in egg mass for the 48 hr exposure interval was significantly greater than all other exposure intervals (Table 1). The changes in mass were less pronounced on wetter substrates, but even so, the control on each of the substrates changed the least whereas the mass of eggs in the 48 hr exposure interval changed the most. The sensitivity of the response of eggs to increased water availability is underscored by the fact that the range of water potentials used was narrow (–60 to –189 kPa).

Eggs containing late-stage embryos exposed to water-saturated substrates for less than 24 hrs also showed evidence of water intake (Fig. 1D–F; Table 1). However, the pattern of mass changes for eggs exposed to water-saturated substrates for 24 or 48 hrs differed between substrates (Table 1). For eggs on wet and intermediate substrates, eggs lost mass in the post-exposure weighing (Fig. 1D, E; Table 1). Eggs exposed for 24 and 48 hrs on dry substrate, on the other hand, increased in mass at the same rates as did those exposed to shorter exposure intervals and at greater rates than the control (Fig. 1F; Table 1).

We performed separate repeated measures ANCOVA on egg mass measurements taken at various stages in incubation for each substrate to examine between-subject and within-subject effects on egg mass suggested by the changes in egg mass apparent in Fig. 1. Clutch (for the intermediate substrate, $F = 13.53, p = 0.0019$) and the interaction between exposure interval and embryonic age (for dry substrate, $F = 11.59$, $p < 0.0001$) were the only significant sources of between-subject variation. This reflected the larger amounts of water taken up by early-stage eggs with longer exposure intervals compared to late-stage eggs (Table 1).

Within-subject effects were most pronounced on dry substrate with all effects (i.e., exposure interval, embryonic age, clutch, and their interactions), except the covariate, being significant ($p < 0.0056$, for nine comparisons). In other words, mass changes through time were greater for late- and early-stage eggs subjected to longer exposure intervals. Only exposure interval (for wet and intermediate substrates, $F = 4.04, p < 0.0001$ and $F = 10.62, p < 0.0001$, respectively) and the interaction between exposure interval and embryonic age (for wet substrate, $F = 3.25$, $p < 0.0001$) were significant sources of variation on the other two substrates.

We also compared hatchling mass and incubation period with mixed model ANCOVA. Among fixed effects including embryonic age, exposure interval, and their interactions, only embryonic age accounted for a significant amount of the variance for hatchling mass and then only for the intermediate substrate ($F = 12.95, p = 0.0041$). Hatchlings from eggs on the intermediate substrate that were exposed to water-saturated substrates early in incubation were heavier than those exposed late in incubation. Clutch, a random effect, and its interaction with the fixed effects had no significant influence on variance in hatchling mass ($p > 0.0658$).

In contrast, exposure interval had a significant effect on variance in incubation period for eggs on both the wet and intermediate substrates ($F = 5.38, p = 0.0010$ and $F = 8.32$, $p < 0.0001$, respectively). For the wet substrate, incubation period for eggs exposed to water-saturated substrates was longer than for the control. Mean incubation period ranged from 54.8 days for the 6 hr exposure interval to 57.3 hrs for the 24 hr interval. Mean incubation period for the control was 53.8 days. On the intermediate substrate, the significant

Table 1. Comparison of pre- to post-exposure changes in egg mass (g) for embryos on dry, intermediate, and wet substrates.

Early-stage	Substrate: Dry			Intermediate			Wet		
Interval	A	B	C	A	B	C	A	B	C
48 hour	0.46			0.36			0.36		
24 hour		0.24			0.25			0.29	
12 hour		0.24			0.27				0.23
6 hour		0.21			0.26			0.31	
1 hour		0.21			0.18				0.24
control			0.02			0.13			0.15
				A__B			A__B		
					B__C			B__C	

Late-stage	Dry					Intermediate			Wet				
Interval	A	B	C	D	E	A	B	C	A	B	C	D	E
48 hour		0.27						-0.02					-0.26
24 hour				0.11				-0.15				-0.13	
12 hour		0.30				0.43				0.37			
6 hour	0.33					0.47			0.57				
1 hour			0.22			0.51				0.30			
control					-0.07		0.14				0.02		
	A_B										C_D		
		B_C											

Significance levels interconnected by a bar do not differ statistically from each other, levels not directly connected by a bar differ statistically ($p < 0.05$). For example, in early-stage embryos on dry substrate, levels A vs. B, B vs. C, and A vs. C all differ significantly, but the changes within level B do not differ from each other; on intermediate substrate, levels A vs. C differ significantly, but A vs. B, B vs. C, and within B do not.

effect due to exposure interval was the result of an unusually long mean incubation period for eggs in the 6 hr interval. Mean incubation period for these eggs was 56.8 days compared to the next longest mean incubation period of 55.1 hrs for 48 hr interval eggs.

DISCUSSION

No previous study has compared the relative sensitivity to flooding of early- and late-stage embryos of any chelonian species. Therefore, we cannot know whether our finding of reduced survivorship among late-stage embryos is typical. If our results are typical for other chelonian species, then nest inundation at later stages of embryogenesis should be more detrimental to embryonic survival than nest inundation at earlier stages.

Flooding and inundation of nests are common enough phenomena that one turtle, *Chelodina rugosa,* has adapted its life cycle to take advantage of flooding. This Australian species lays its eggs underwater where they remain arrested in an early state of development until seasonally flooded billabongs recede (Kennett et al., 1993a, 1993b). Other turtles may select elevated nest sites and avoid possible failure due to flooding (Plummer, 1976; Cox and Marion, 1978). *Trachemys scripta* in Panama apparently time their nesting to take advantage of wet season rains to allow the escape of hatchlings from the nest as well as to avoid inundation during embryonic development (Moll and Legler, 1971).

Other tropical turtles (*Podocnemis unifilis* and *P. expansa*) nest on sand beaches exposed by receding rivers during the dry season, but have short incubation periods that allow emergence of hatchlings before river levels rise in response to seasonal increases in rainfall (Alho and Pádua, 1982; Thorbjarnarson et al., 1993). In contrast, *Dermatemys mawii* from Belize nests at or close to the waterline during the flood season, but has a long incubation period (Polisar, 1996). The early-stage eggs of this species may be unusually tolerant of submergence because one clutch survived simulated nest flooding for 36 days (Polisar, 1996).

Consequently, adaptations in nest timing to local, predictable hydrologic regimes may be expected when other environmental factors allow successful incubation. Ideally, turtles should time nesting so that embryogenesis, particularly its later stages, occurs at a time when nest flooding is least likely. Studies of the timing of nesting relative to hydrologic patterns are few (e.g., Moll and Legler, 1971; Alho and Pádua, 1982; Kushlan and Jacobsen, 1990; Kennett et al., 1993a, 1993b; Thorbjarnarson et al., 1993; and Polisar, 1996).

We plotted the nesting season for *T. scripta* from our study area on a hydrograph for the Mississippi River near its confluence with the Illinois River where most of our turtles were collected (Fig. 2). Although undoubtedly also associated with other environmental variables, nesting coincided closely with the end of the spring flood pulse for hydrological data collected prior to the impoundment of the river by Lock and Dam 26 in 1938.

The impact of the alteration of the natural hydrologic regime was clearly demonstrated during the flood of 1993 (Fig. 2). Normally, maintenance of a 9-foot channel for navigation effectively keeps the river at artificially high levels and suppresses the flood pulse. During 1993 the combination of the effects of unusually heavy rainfall (a natural event) and the preceding maintenance of a 9-foot

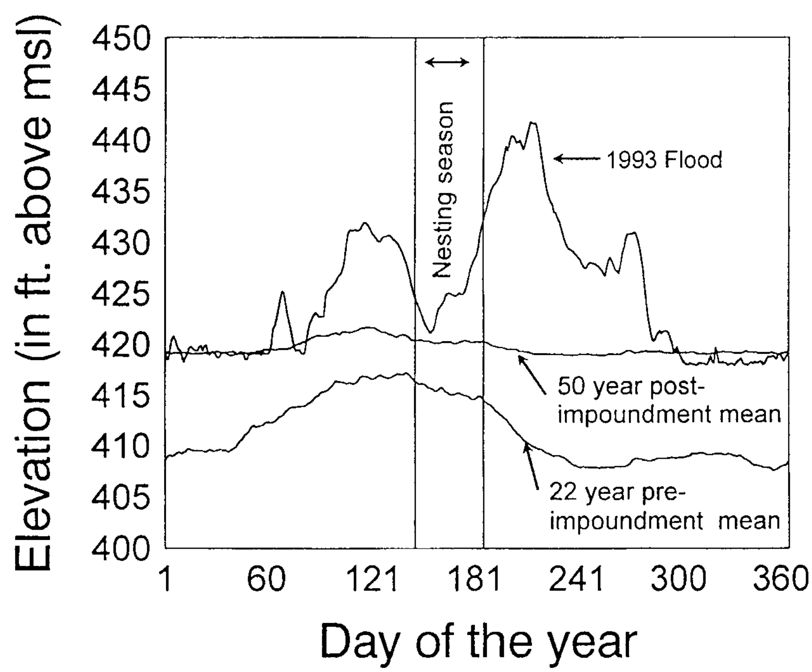

Figure 2. Hydrograph of river levels of the Mississippi River near the study site. Separate tracings reflect: 1) 1993 flood levels; 2) 50-year (1939–89) mean levels post-impoundment Lock and Dam 26 in 1938; 3) 22-year (1915–37) mean levels pre-impoundment. Nesting season for *Trachemys scripta* in 1994 is superimposed. Elevation is in feet above mean sea level; day of year is Julian date.

navigation channel made the resulting flood levels higher than they would have been, given the historically natural pattern in river levels prior to impoundment. Several nesting localities in the study area were inundated, and the nests in those localities were destroyed. The dramatic increase in mortality that we observed among our experimental eggs during the later stages of development underscores the importance of timing nesting to avoid inundation. The alteration of natural hydrologic patterns because of navigation and flood control dams may increase nesting failures even in years without extreme flood events, although this has not been studied. Clearly, investigations of nesting patterns in relation to hydrologic regimes will be important in predicting the effects of stream modification on chelonians.

The primary purpose of our study was to compare responses of early- and late-stage embryos to water-saturated substrates, because nearly all previous studies concentrated on the effects of flooding on early-stage embryos. Our study does not consider the possible impact of embryonic diapause (Ewert, 1985) on the response of embryos to flooding or water-saturated substrates.

Embryonic diapause is a mechanism that prolongs the egg stage making the egg a refuge for the embryo (see Ewert, 1985; Ewert and Wilson, 1996). Ewert (1985) suggested that a diapausing embryo should be able to escape certain crises such as flooding. At present no experimental study has examined the effect of diapause on embryonic survival of flooding. However, early-stage embryos of *T. scripta*, a species without embryonic diapause, are more resistant to flooding than are older embryos. Diapause in those species that display it occurs at a relatively early embryonic stage (Ewert, 1985; Ewert and Wilson, 1996). Consequently, separation of the effect of diapause *per se* from that of embryonic age on survival of flooding will be difficult.

The structure of the egg shell (i.e., brittle-shelled vs. flexible-shelled) may also be an important variable. Because the embryos of species with brittle-shelled eggs are less affected by variations in the hydric environment during incubation than are species with flexible-shelled eggs (see Packard, 1991), the response to flooding of species that lay brittle-shelled eggs may differ fundamentally from those that lay flexible-shelled eggs. Although no experimental study has examined interspecific survivorship of embryos of equivalent age, species that lay brittle-shelled eggs may be more resistant to flooding than those that lay flexible-shelled eggs. For instance, at least some 1- to 12-day-old embryos of *Apalone mutica* survived immersion for 8 days (Plummer, 1976). In contrast, all 19-day-old embryos of *Pseudemys nelsoni* died after immersion for 6 days, and few survived immersion for 3 days (Kam, 1994).

Although access to environmental water is critical to embryonic development in flexible-shelled eggs (Ewert, 1985; Packard, 1991), adsorption of excess amounts of water during immersion may interfere with development and even cause bursting of eggs (Ewert, 1985). Importantly, some of the embryos of *P. nelsoni* immersed for longer intervals did not die during immersion but continued development and then died prior to hatching (Kam, 1994). Whether such delayed mortality also occurs among species laying brittle-shelled eggs is not known but could be investigated experimentally. We did not observe any delayed mortality among the early-stage eggs of *T. scripta elegans* that we studied. However, we did not expose them to as long an immersion interval as did Kam for the *P. nelsoni* eggs that he studied.

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